COMMENTS ON THE OSTEOLOGY OF BALISTOID FISHES (TETRAODONTIFORMES), WITH NOTES ON THE TRIODONTID PELVIS

James C. Tyler and Keiichi Matsuura

Abstract.—Two workers recently have independently described the osteological structure of cleared and stained specimens of a large number of genera and species (ca. half the same) of fishes of the families Balistidae and Monacanthidae (the superfamily Balistoidea, Tetraodontiformes). The phylogenetic and classificatory conclusions reached by Matsuura (1979) and Tyler (1980) are rather similar, as are the majority of their osteological observations. The few differences (ca. 5%) in their anatomical reports are discussed herein.

Introduction

Matsuura (1979) published a detailed osteologically based phylogenetic study of the balistoid fishes (Balistidae, triggerfishes; Monacanthidae, filefishes) utilizing cleared and alizarin stained specimens of 15 species representing 11 genera of balistids and 28 species representing 22 genera of monacanthids. In his similarly based study Tyler (1980) used 21 species representing 11 genera of balistids and 32 species representing 17 genera of monacanthids. Matsuura's coverage includes 57% of the balistids and 44% of the monacanthids treated by Tyler, while Tyler's coverage includes 80% of the balistids and 50% of the monacanthids treated by Matsuura. Thus, of the total of 70 species and 36 genera of balistoids treated by either Matsuura or Tyler, 26 species and 25 genera are shared between the two (Table 1). The species studied by Matsuura are mainly from Japan and the western Pacific, while those used by Tyler are of more worldwide localities.

Since Matsuura and Tyler worked independently of one another, and are of somewhat different (although cross-fertilized) cultural schools of ichthyology, yet studied osteologically many of the same species and genera, an opportunity to test the degree of similarity of their materials and observations presents itself. If one assumes that both researchers were careful in their observations and precise in their descriptions, then similar results can be presumed to be accurate in the vast majority of cases, for it is unlikely that two attentive workers would frequently commit the same observational error independently. Therefore, only the few differences in the osteological descriptions of Matsuura and Tyler need to be discussed to clarify or rectify these observations for the benefit of subsequent workers. The latter will

Table 1.—List of species studied (X) by Matsuura (1979) and Tyler (1980), and indication of synonyms.

| Species | Examined by: | |
	Matsuura	Tyler
Balistidae		
Abalistes stellatus	X	X
Balistapus undulatus	X	X
Balistes capriscus	—	X
Balistes forcipatus	—	X
Balistes polylepis	—	X
Balistes vetula	X	X
Balistoides conspicillum	X	X
Balistoides viridescens	—	X
Canthidermis maculatus	X	X
Sufflamen bursa	X	X
= *Hemibalistes bursa*		
Sufflamen chrysopterus	X	X
= *Hemibalistes chrysopterus*		
Melichthys niger	—	X
Melichthys vidua	X	X
Odonus niger	X	X
Pseudobalistes flavomarginatus	X	—
Pseudobalistes fuscus	X	—
Rhinecanthus aculeatus	X	X
Rhinecanthus echarpe	X	X
= *Rhinecanthus rectangulus*		
Rhinecanthus verrucosus	—	X
Sufflamen fraenatus	X	X
Sufflamen verres	—	X
Xanthichthys lineopunctatus	—	X
Xanthichthys mento	X	—
Xanthichthys ringens	—	X
Monacanthidae		
Acanthaluteres spilomelanurus	—	X
Acreichthys hajam	X	—
Alutera heudelotii	X	X
Alutera monoceros	X	X
Alutera schoepfi	X	X
Alutera scripta	X	X
Amanses scopas	X	X
Anacanthus barbatus	X	X
= *Psilocephalus barbatus*		
Arotrolepis filicaudus	X	—
Brachaluteres trossulus	—	X
Brachaluteres ulvarum	X	—
Cantherhines dumerili	X	—
Cantherhines pardalis	—	X
Cantherhines pullus	—	X

Table 1.—Continued.

Species	Examined by:	
	Matsuura	Tyler
Cantherhines sandwichiensis	—	X
Chaetoderma penicilligera	X	X
= *Chaetoderma spinosissimus*		
Eubalichthys mosaicus	X	—
Laputa cingalensis	—	X
Meuschenia freycineti	X	—
Meuschenia hippocrepis	X	—
Meuschenia trachylepis	X	—
Monacanthus chinensis	X	X
Monacanthus ciliatus	—	X
Monacanthus mylii	—	X
Monacanthus tuckeri	—	X
Navodon modestus	X	—
Navodon setosus	—	X
Navodon tesselatus	X	—
Nelusetta ayraudi	X	—
Oxymonacanthus longirostris	X	X
Paraluteres prionurus	X	X
Paramonacanthus barnardi	—	X
Paramonacanthus cryptodon	—	X
Paramonacanthus curtorhynchus	—	X
Paramonacanthus japonicus	X	—
Pervagor melanocephalus	X	X
Pervagor spilosomus	—	X
Pseudalutarius nasicornis	X	X
= *Pseudaluteres nasicornis*		
Pseudomonacanthus peroni	X	—
Rudarius ercodes	X	X
Rudarius minutus	—	X
Scobinichthys granulatus	X	—
Stephanolepis auratus	—	X
Stephanolepis cirrhifer	X	X
Stephanolepis hispidus	—	X
Stephanolepis setifer	—	X

have the opportunity to test in the arena of the 95% agreement between Matsuura and Tyler what is here considered the likely assumption that they are relatively careful reporters. It is here postulated that only about 5% of the osteological observations of Matsuura and Tyler are in any kind of conflict.

Even though Matsuura attempted a cladistically based analysis which should exclusively use shared advanced character conditions (cladistic approach) to link groups in phylogenetic interpretations and generic segrega-

tions, while Tyler utilized the weighting and balancing of both generalized and specialized features (gradistic or phenetic approach) to the same end, the phylogenetic conclusions and generic recognitions between these two osteologically based works are rather similar, with only a few notable exceptions (e.g., see *Canthidermis*, below).

The differences in the interpretative methodologies are not discussed further here, with the following comments confined to the differential osteological observations. Most of these are accountable to statements about genera based on different sets of species examined, or to different sizes of individuals of the same species examined for what prove to be ontogenetic features, and to individual variation between specimens of the same species.

Unless otherwise stated, references are to Matsuura (1979) and Tyler (1980).

Balistidae

Frontal of Abalistes stellatus.—Matsuura states (p. 112, Fig. 40) that this species is unique among the balistids in "having the frontal expanded greatly . . . posteriorly beyond the level of the rounded postero-dorsal surface of the cranium," while Tyler makes no such distinction. The explanation is undoubtedly that Matsuura's three specimens were all large adults (200.0–230.2 mm SL) while Tyler's single specimen was much smaller (87.6 mm SL) and did not yet possess this posterolateral expansion of the frontal which apparently develops only in larger adults. This region of the skull in the 87.6 mm specimen is very similar to that of most other balistids.

Encasing scales of Balistapus undulatus.—Tyler states (1962, 1980) that this species has but a single pair of scales in Segment III of the encasing scale series at the posterior end of the pelvis, in contrast to two pairs in this segment in *Balistes* [*Verrunculus*] *polylepis, Balistes vetula,* and other balistids; Matsuura states (p. 73) that there are two pairs of scales there in *B. undulatus* as well as in all other balistids. Matsuura examined 11 specimens of 41.8 to 226.0 mm SL and Tyler examined 5 specimens of ca. 120 to 124.3 mm SL. Re-examination of Tyler's material and of 3 additional specimens (USNM 301981, 30.2 mm SL; USNM 197525, 46.0–68.7 mm SL) recently cleared and stained shows Matsuura to be correct. However, there tends to be fusion of the two pairs of scales in Segment III to the extent that it often appears in large specimens that there is a single pair. Thus, in the recently prepared 68.7 mm SL specimen, only a single pair of scales was evident until all of the surface granulations and spiny processes had been shaved away with a scalpel and the scale plates substantially thinned. Only then in transmitted light was it possible to detect the closely apposed surfaces of the two pairs, which even in this relatively small specimen were so consolidated that they nearly fused in places. Re-examination of the 124.3 mm SL specimen previously reported by Tyler as having a single pair of scales in

Segment III shows that this would be more accurately characterized as 1½ pairs (3 pieces), for the two pairs seem fully fused on one side but distinct on the other. In the previously examined 121.6 mm SL specimen, both pairs seem fully fused. It is obvious that Matsuura is correct in pointing out that Segment III has two pairs of scales, at least developmentally, in all balistids, even though some fusion between elements of the pairs can be expected in some (usually larger) specimens of some species (such as *B. undulatus*).

Balistid postcleithrum.—Matsuura states (p. 78) that all balistids he examined have the postcleithrum as two pieces (dorsal and ventral postcleithra), while (p. 80) all monacanthids have the postcleithrum as a single piece. Tyler states (p. 101) that balistids have it as either a single piece or divided into dorsal and ventral segments, in contrast to monacanthids in which the postcleithrum is always a single piece. Tyler gives lateral view illustrations (Figs. 70–72) of the entire skeleton of the balistids *Rhinecanthus echarpe*, *Sufflamen fraenatus*, and *Canthidermis maculatus* showing the postcleithrum as a single piece, in contrast to illustrations (Figs. 51, 69, 73) of *Balistapus undulatus*, *Balistes polylepis*, and *Xanthichthys lineopunctatus* showing the two segments of the postcleithra. Re-examination of the specimens used by both Matsuura and Tyler indicates that Tyler is correct in showing fusion of the postcleithrum into a single piece in some balistids.

Supposed scale bone of Canthidermis maculatus.—Matsuura describes and illustrates (p. 109, Fig. 38) a scale bone as being present in this species alone among all the balistoids, while Tyler (p. 43) says that a scale bone is absent in all balistoids and in all other plectognaths (tetraodontiforms). This is but one example among many of a bone that is present in such possibly ancestral or sister group perciforms as acanthuroids and chaetodontoids but lost by plectognaths in their largely reductive evolutionary processes. Matsuura's two specimens were large adults (218.4 and 251.5 mm SL), while Tyler's was an especially nicely cleared 80.1 mm SL specimen, for which a lateral view illustration of the entire skeleton is presented, and one larger (216.9 mm SL) specimen. Tyler's illustration (Fig. 72) shows a bone similar to that thought to be a scale bone by Matsuura. Notes on the original drawing state that this is simply the posterior portion of the sphenotic, which superficially, on the lateral surface of the skull, is separated from the more anterior portion of the sphenotic by a ventrad extension of the frontal. The frontal makes slight contact with a dorsad extension of the pterotic and apparently divides the sphenotic into an anterior and posterior portion which are still fully continuous just below the surface. The 80.1 mm specimen has been especially carefully re-examined to verify this point, and the ventrad extension of the frontal that overlies the middle of the lateral surface of the sphenotic laid back and excised on one side. This reveals (Fig. 1) the depression on the sphenotic that accommodates the extension of the frontal. The
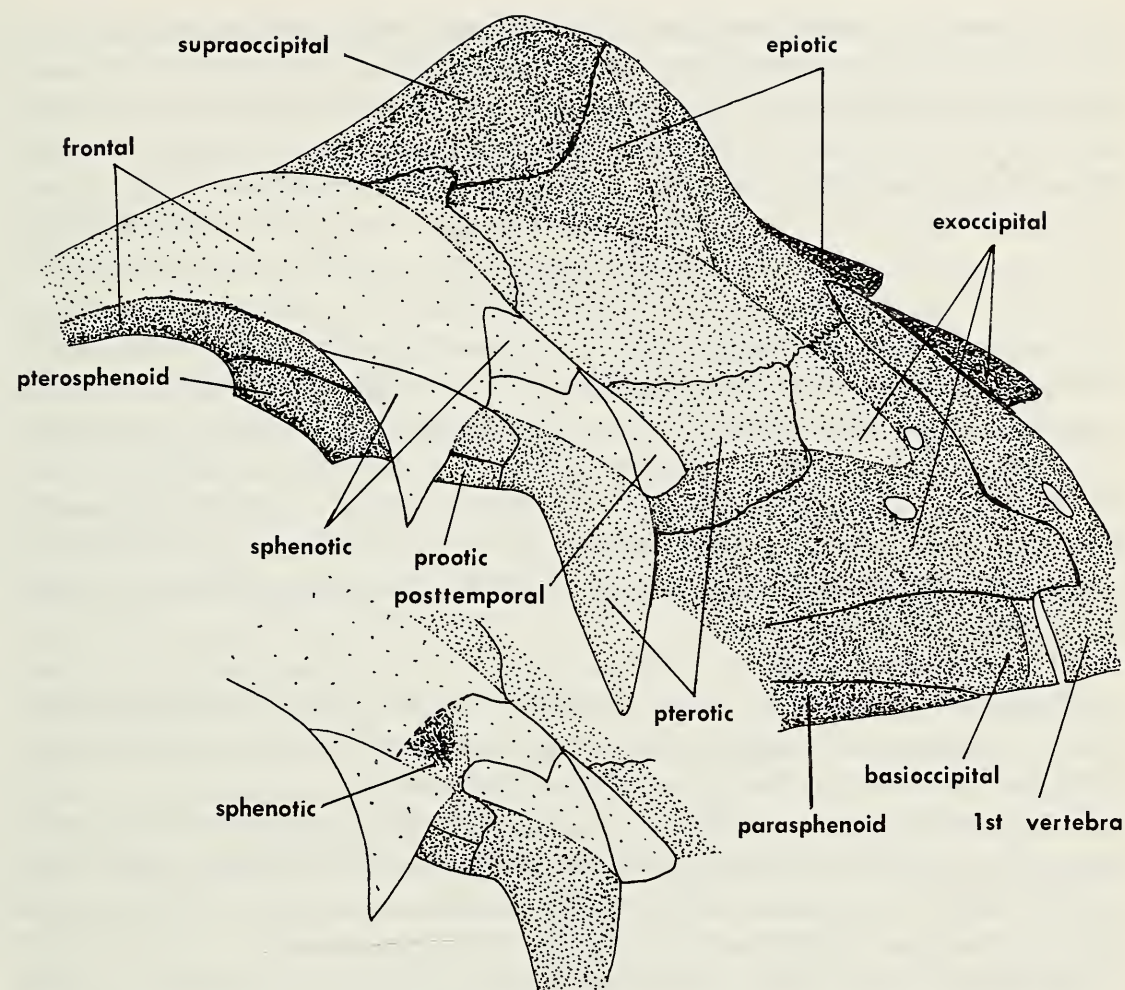
Fig. 1.   Posterior portion of cranium of *Canthidermis maculatus*, ANSP 100085, 80.1 mm SL. Larger drawing above shows the downward flange of the frontal meeting the upward extension of the pterotic, superficially dividing the sphenotic into forward and rear sections which are clearly continuous below the surface as seen in the lower drawing in which the downward flange of the frontal has been cut away (dashed line).

more posterior portion of the apparently divided sphenotic could be mis-interpreted as a scale bone. Re-examination of the specimens used by Mat-suura also shows the element described as a scale bone to be the rear of the sphenotic.

This separation of the sphenotic by a superficial meeting of a ventrad flange of the frontal and a dorsad flange of the pterotic also occurs to some degree in at least large individuals of *Balistes capriscus* (Tyler, Fig. 74) with partial external separation, in *Sufflamen fraenatus* (Tyler, Fig. 70) with partial external separation, and in *Balistes polylepis* (Tyler, Fig. 69) with external separation as complete as in *Canthidermis*.

Matsuura placed great emphasis on the supposed presence of a scale bone

in *C. maculatus* as an indicator of its primitiveness, and separated it off first (Fig. 79) as the sister group of all other balistids on this basis. Fraser-Brunner (1935:660–661) also thought *Canthidermis* to be the most generalized balistid, but only on the basis of it lacking enlarged tympanic scales above the pectoral fin. Conversely, Tyler (p. 123) considered *Canthidermis* to be only slightly less specialized than the most specialized of the balistids (the *Xanthichthys-Odonus* line) and of about the same level of specialization in its own way as *Melichthys*. Tyler considered *Canthidermis* specialized for a more oceanic and pelagic existence than the other balistids (even more so than *Abalistes*, an offshore form) with the scales of the body "all being reduced in size and nonoverlapping [explaining the absence of distinctive tympanic scales] and thus more flexible . . ." and "also specialized in having the full ossification of the skeleton much delayed, as well as in having the most rudimentary pelvic apparatus among the balistids," including its especially rudimentary pelvic fin ray element and relatively inflexible series of encasing scales.

Balistoid urohyal shape.—Matsuura (p. 92 *et seq.*, Figs. 26, 28) describes a difference between the urohyal in balistids (plate-like with several projections) and monacanthids (flattened and boomerang-like) overlooked by Tyler in his comparative diagnoses of the two families.

Balistid epipleurals.—Matsuura states (p. 149) that the epipleurals in balistids never extend posteriorly beyond the first caudal vertebra, while Tyler (p. 167, Fig. 71) correctly shows that in *Rhinecanthus* they are attached as far posteriorly as the fifth and sixth caudal vertebrae.

Balistoid posttemporal.—Both Matsuura and Tyler call attention to a familial distinction in the posttemporal between balistids and monacanthids, but describe it with different emphasis. Matsuura states (p. 148–149) that the posttemporal in balistids articulates with the epiotic, but that it does not contact that bone in monacanthids. Tyler (p. 101, 135) states that the posttemporal in balistids is held in a deep groove on the lateral surface of the pterotic, but that in monacanthids it is held more superficially in a much less deep groove on the lateral surface of the pterotic. Tyler makes no direct statement on the relationship of the posttemporal to the epiotic. Matsuura is correct in pointing out that the less sturdy posttemporal of monacanthids is usually distinctly farther removed from the epiotic (least so in *Oxymonacanthus*, see Matsuura Fig. 47 and Tyler Fig. 122) than in balistids. In some specimens of some species of balistids, however, it appears that the posttemporal either does not make contact with the epiotic or barely does so (see Tyler, Fig. 52, for *Balistapus undulatus*). It is excluded, or mostly so, from that contact by the juncture of the sphenotic and pterotic behind it, which intervenes between the posttemporal and epiotic. Perhaps there are ontogenetic changes in the degree of exclusion. The proximity of the

posttemporal to the epiotic in balistids is sometimes closer as seen from the inside of the cranium (cephalic vault) since the sphenotic and pterotic overlap the posterodorsal end of the posttemporal less extensively internally than externally. In any case, the relationship of the posttemporal to the epiotic is more of a quantitative than a qualitative distinction between the two families.

Monacanthidae

Monacanthid scapular foramen.—Matsuura states (p. 80) that "the inner surface of the scapula foramen is completely enclosed by the scapula in all the monacanthid members, though the anterior edge of the outer surface of the scapula foramen is surrounded by the cleithrum in these members: *Stephanolepis, Rudarius, Alutera, Oxymonacanthus, Pseudalutarius,* and *Anacanthus,*" whereas Tyler states (p. 172) that the scapular foramen is completely enclosed by the scapula in all monacanthids (as in balistids) except *Anacanthus* and *Pseudalutarius,* two of the most specialized genera of the family. Re-examination of the specimens used by Tyler, including the careful disarticulation of the delicate scapula from previously undisturbed pectoral girdles, reaffirms that the scapula is incomplete around the foramen (Fig. 2) anteriorly in *A. barbatus* and *P. nasicornis,* where the border of the foramen is formed by the cleithrum. However, there is individual variation in the closure of the foramen, for re-examination of Matsuura's specimens (4 of *P. nasicornis,* 124.3–150.2 mm SL; 2 of *A. barbatus,* 157.1–206.4 mm SL), all of which are slightly to substantially larger than those used by Tyler (2 of *P. nasicornis,* 50.8–108.3 mm SL; 3 of *A. barbatus,* 142.3–138.7 mm SL) shows the foramen sometimes to be complete.

Monacanthid pharyngobranchial and basibranchial elements.—Matsuura extensively surveyed and amply illustrated the branchial arches in balistoids, probably more fully than ever before with any familial grouping of fishes. Tyler's interpretations of the branchial arches differ in only two respects. Matsuura states (p. 102–103) that *Oxymonacanthus longirostris* and *Paraluteres prionurus* are unique among the monacanthids in having a toothless suspensory first pharyngobranchial in addition to the two toothed elements found in all other monacanthids, and that *P. prionurus* is also unique in having four basibranchials rather than the three of all other monacanthids (except *Anacanthus* with only two). By omission to the contrary, Tyler implies that both of these species have the normal monacanthid branchial arrangement of only two pharyngobranchials (both toothed) and three basibranchials.

Re-examination of Tyler's specimens of these two species (8 of *O. longirostris* and 1 of *P. prionurus*) indicates that none of them has a first toothless suspensory pharyngobranchial and that *P. prionurus* has only three
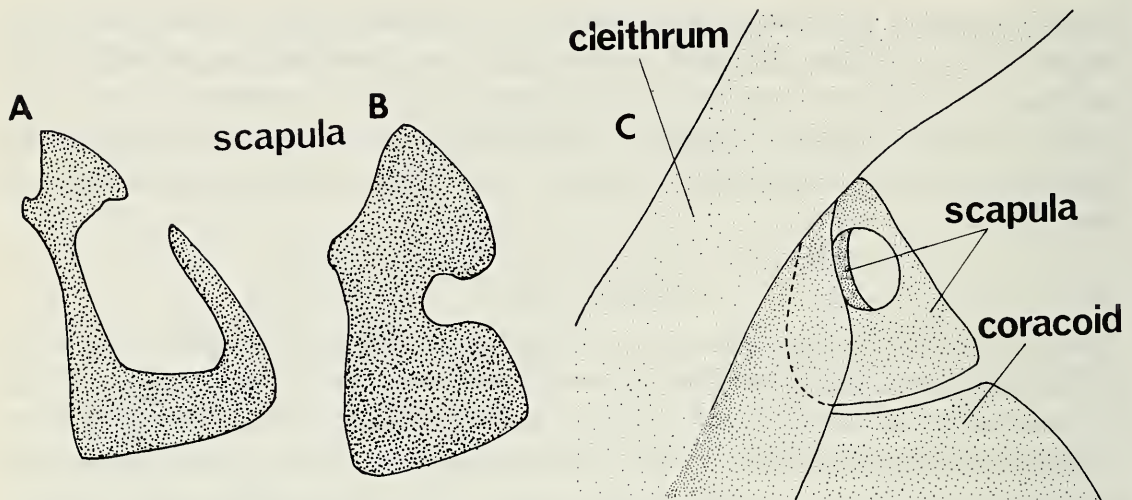
Fig. 2.   Medial view of left scapula of (A) *Pseudalutarius nasicornis*, USNM 294075, 50.1 mm SL, and (B) *Anacanthus barbatus*, ANSP 109648, 142.3 mm SL, in contrast to the more normal condition of the scapula (C) as seen, for example, in *Alutera monoceros*, HUMZ 38062, 155.2 mm SL, in lateral view.

basibranchials, as do most other monacanthids. Re-examination of Matsuura's specimens (2 of *O. longirostris* and 2 of *P. prionurus*) shows that the element described as the toothless suspensory first pharyngobranchial is actually a distal part of the first epibranchial. This distal part is abnormally separated from the proximal part of the first epibranchial by an unossified portion. Examination of additional specimens of *O. longirostris* (HUMZ 40658, 50366) confirms the normal pharyngobranchial arrangement in this species, with two pharyngobranchial elements only, both toothed. Re-examination of Matsuura's specimens of *P. prionurus* indicates that the bone interpreted as the fourth basibranchial is actually the anterior portion of the fourth ceratobranchial, abnormally fused into a shaft-like element and separated from its posterior region by an unossified segment.

To avoid confusion, it should be noted that there is a typographical error in Table 4 (p. 108) of Matsuura's work, for *Paraluteres* is listed as having the normal two pharyngobranchials, while it is described in the text (p. 108) and illustrated (Fig. 34) as having three pharyngobranchials.

Posttemporal of Anacanthus barbatus.—Tyler states (p. 167) that the "posttemporal is present in all monacanthids except *Psilocephalus barbatus*, none of the three adult specimens of which shows any evidence of one. Whether the ossification center for the posttemporal is lost or incorporated indistinguishably with that of the pterotic remains problematical," while Matsuura (p. 116) has been able to distinguish a bump on the pterotic in his specimens [*Anacanthus*] which may represent the fused posttemporal.

Dewlap expansion in monacanthids.—Matsuura states (p. 77) that "In

contrast with the primitive monacanthids, the advanced monacanthids such as the fishes of the genus *Brachaluteres* can only slightly extend downward the reduced pelvis without the incasing scales, however, they have the other mechanism to inflate their abdomen'' [=inflatable stomach]. This statement was made to explain the functional significance of the stomach of *Brachaluteres*. However, it should be borne in mind that one of the most highly specialized of all monacanthids, the exceptionally elongate *Anacanthus*, which is like the deep bodied *Brachaluteres* in its very weakly developed pelvis without encasing scales, can flare one of the largest dewlaps among all of the monacanthids, generalized and specialized. The ability to flare a dewlap is of little phylogenetic significance.

Third tooth of dentary in monacanthids.—Matsuura states (p. 83) that the third or posteriormost (last) tooth in the dentary "is extremely reduced in size" in *Brachaluteres* (*ulvarum* examined) and *Pseudomonacanthus* (*peroni*), and absent altogether in *Rudarius* (*ercodes*), *Oxymonacanthus* (*longirostris*), *Paraluteres* (*prionurus*), and *Anacanthus* (*barbatus*). Tyler states (p. 173) that the third tooth of the dentary is much smaller than the others in *Pseudalutarius* (*nasicornis*), and absent altogether in *Rudarius* (*ercodes* and *minutus*), *Oxymonacanthus* (*longirostris* examined, and presumably in *halli* also), *Paraluteres* (*prionurus*), *Anacanthus* (*barbatus*), and *Brachaluteres* (*trossulus* examined, and presumably in *baueri* and *wolfei* also), while Tyler did not examine *Pseudomonacanthus*. It seems obvious on the basis of these two reports that the development of the third dentary tooth is variable within *Brachaluteres,* being reduced in size in the species (*ulvarum*) studied by Matsuura and absent in that (*trossulus*) studied by Tyler or reported in the literature (*baueri* and *wolfei*), and that it is absent in all species of *Rudarius, Oxymonacanthus, Paraluteres* and *Prionurus*.

This leaves in conflict the reported size of the third dentary tooth of the monotypic *Pseudalutarius* (*nasicornis*). Matsuura shows it (Fig. 22) to be of relatively large size in the illustrated individual among his four specimens of 124.3–150.2 mm SL, whereas Tyler reports this tooth as of much reduced size in his two smaller specimens (50.8–108.3 mm SL). As a check on variability in the size of the third dentary tooth in *Pseudalutarius nasicornis,* an additional specimen has been cleared and stained (USNM 294075, 50.1 mm SL), and it too has the third dentary tooth much reduced in size (Fig. 3, left) as reported by Tyler. On the other hand, re-examination of Matsuura's specimen of this species (HUMZ 38074, 150.2 mm SL) confirms that the third tooth is relatively larger (Fig. 3, right). There obviously is variation in the size of the third dentary tooth in this species, and it may increase with increasing specimen size.

Ribs of Pseudalutarius nasicornis.—Matsuura describes (p. 140) the rib-
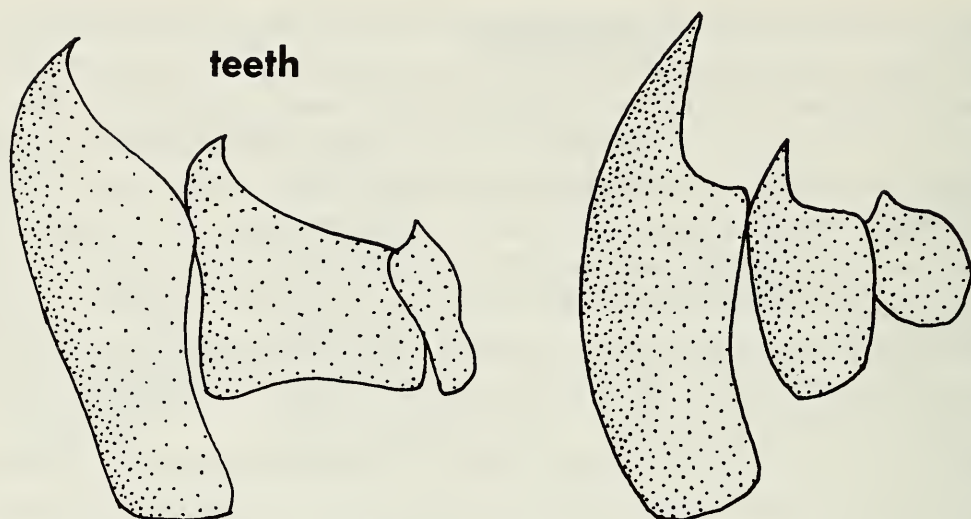
Fig. 3.   Lateral view of teeth in left dentary of *Pseudalutarius nasicornis*, USNM 294075, 50.1 mm SL (left) and HUMZ 38074, 150.2 mm SL (right), to show the variation in size of the third (posteriormost) tooth; anterior to left.

like element attached to the first vertebra as an epipleural, and so illustrates it (Fig. 56). Conversely, Tyler (p. 167) states that the element attached to the first vertebra is a pleural rib like those that follow it on the other abdominal vertebrae, and so illustrates it (Figs. 114, 123). Re-examination of Matsuura's four specimens and of an additional recently cleared and stained specimen (USNM 294075, 50.1 mm SL) indicates that the element attached to the first vertebra should be recognized as a pleural rib rather than an epipleural, for the following reasons: 1) the element is longer than the epipleurals that are attached to the pleural ribs of the second to seventh vertebrae; 2) the element and the pleural ribs are distinctly more ventrally directed in position than are the epipleurals; 3) the element is in positional orientation and symmetrical series with the other pleural ribs (second to seventh vertebrae); 4) the element courses along the peritoneal wall of the abdominal cavity like the other pleural ribs, rather than, as with the series of epipleurals, being in the septum between the epaxial and hypaxial musculature.

Matsuura also states (Table 9, p. 139) that the epipleurals in monacanthids other than *Pseudalutarius* (including in *Rudarius ercodes* and *Brachaluteres ulvarum*), start on the second abdominal vertebra, while Tyler (p. 167) says and illustrates that they usually start from the second abdominal vertebra, but that they start from the third vertebra in *Rudarius ercodes* and *R. minutus* as well as in the single species he examined of *Brachaluteres* (*trossulus*). Re-examination of Matsuura's specimens of *R. ercodes* and *B. ulvarum* confirms Matsuura's statements. Thus, there is occasional variation between species and between individuals of the same species in the place

of origin of the first epipleural, variously from the second abdominal vertebra (usually) or from the third (more rarely).

Second dorsal spine of Brachaluteres.—Matsuura states (p. 126) that all monacanthids have two dorsal spines, except *Anacanthus* which has only one, while Tyler says (p. 146) that both *Brachaluteres* and *Anacanthus* have only a single dorsal spine. The conflict is between the species studied of *Brachaluteres*, Matsuura examining *B. ulvarum,* in which a second spine is present, and Tyler examining *B. trossulus,* in which it is absent. Tyler should have known this, for he had radiographed the two co-types of *B. ulvarum* (Stanford University 7128, now California Academy of Sciences), as reported in his table of plectognath vertebral counts, and the radiographs clearly show a small but normally developed second spine to be present. The second spine is absent in two cleared and stained and 20 radiographed specimens of *B. trossulus* studied by Tyler.

Upper free hypural in monacanthids.—Matsuura states (p. 147) that an upper free hypural is absent in *Rudarius ercodes, Brachaluteres ulvarum,* and in adult *Alutera scripta.* Tyler reports (p. 173, 179, *et seq.*) the uppermost hypural to be free in *Alutera scripta* and the other three species of *Alutera* he examined (*heudelotii, monoceros* and *schoepfi*) as well as in *Brachaluteres trossulus,* but to be absent in most specimens studied of *Monacanthus ciliatus,* both species studied of *Rudarius* (*ercodes* and *minutus*), and in *Amanses scopas.* Matsuura describes (p. 147) and illustrates (Fig. 66) an upper free hypural in a juvenile *Alutera scripta* and its absence (through fusion) in an adult. Matsuura's four specimens of *A. scripta* were 59.0–295.8 mm SL and the two of Tyler were 46.2–73.3 mm SL. Fusion of the upper free hypural obviously occurs with increasing specimen size in *A. scripta* and in other species of monacanthids.

Palatine of Anacanthus barbatus.—Matsuura emphasizes (p. 88) the unique close articulation of the palatine with the ectopterygoid in *Anacanthus barbatus,* which is a more distant articulation mediated by a strong ligament of varying length in all other monacanthids. Both Matsuura (Fig. 25) and Tyler (Figs. 110, 120) illustrate this close apposition of articulation in *A. barbatus,* but Tyler does not comment on it in the text.

Pelvis-pectoral girdle articulation in Pervagor.—Tyler (p. 180, Fig. 105) comments on a unique specialized feature of the pelvis in *Pervagor* not mentioned by Matsuura, this being the development on the anterior region of the pelvis, just behind the pectoral girdle, of a lateral knob-like expansion which articulates with a similar expansion on the posterior edge of the coracoid, forming a point of pivot around which the pelvis rotates.

Encasing scales of Chaetoderma penicilligera.—Matsuura states (p. 59) that there are three series of encasing scales at the end of the pelvis in *C. penicilligera* and so illustrates it (Figs. 7–8), while Tyler describes (p. 178, Fig. 88) only two series of encasing scales in this species. Examination of
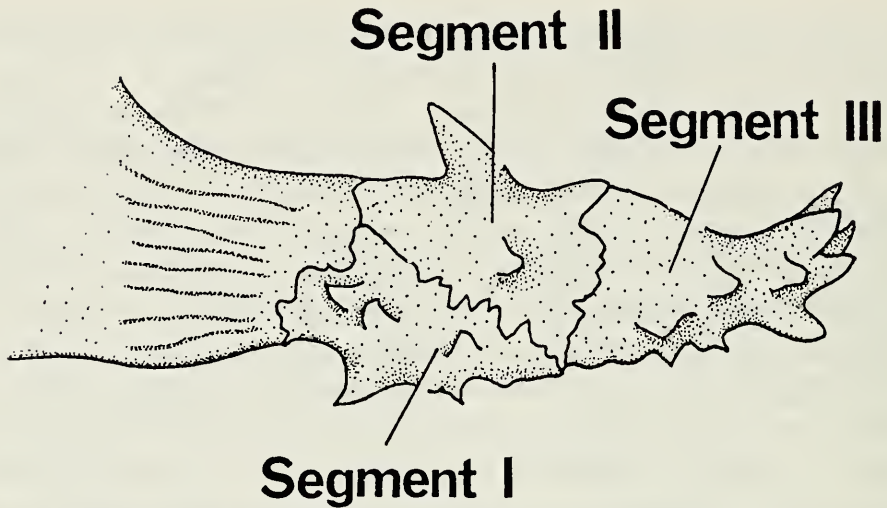
Fig. 4.   Lateral view of encasing scales at end of pelvis (anterior to left) of *Chaetoderma penicilligera*, HUMZ 40645, 172.3 mm SL.

an additional specimen of *C. penicilligerum* (HUMZ 40645, 172.3 mm SL) clearly shows the encasing scales in three series (Fig. 4), although the second segment is not broadly present on the ventral surface of the apparatus.

Triodontidae

Pelvis of Triodon.—Matsuura presents an extensive survey of the pelvic apparatus of balistoids, greatly expanding on the coverage provided by Tyler (1962, 1980), especially for the rudimentary fin ray element. The latter lies buried beneath encasing scales and is difficult to dissect free for detailed study and illustration. As an aside to that exposition on the balistoid pelvic apparatus, Matsuura describes the pelvis of *Triodon,* the most generalized Recent member of the gymnodont line of plectognaths. Matsuura states (p. 78) that there is a "very small cartilage plug which is quite similar to the structure found in the advanced monacanthids" although "it is very difficult to locate since the plug is tightly enclosed by tough connective tissue at the end of the posterior part of the pelvis." In Tyler's descriptions (1962, 1980) of the pelvis in *Triodon* no mention is made of these or of most other cartilaginous elements of the skeleton.

Re-examination of one (ANSP 98917, 463.3 mm SL) of the two specimens of *Triodon* previously studied by Tyler shows that cartilaginous plugs exist at both the anterior and posterior ends of the pelvis (Fig. 5). The plugs surround the paired ends of the pelvis, as one would expect in an endochondral bone of a plectognath. Each plug is bilaterally paired, with the two halves of the plug bound together by connective tissue and terminating both anteriorly and posteriorly the ossifications of the pelvis (which two halves are fused together in much of the posterior half of their lengths but not at
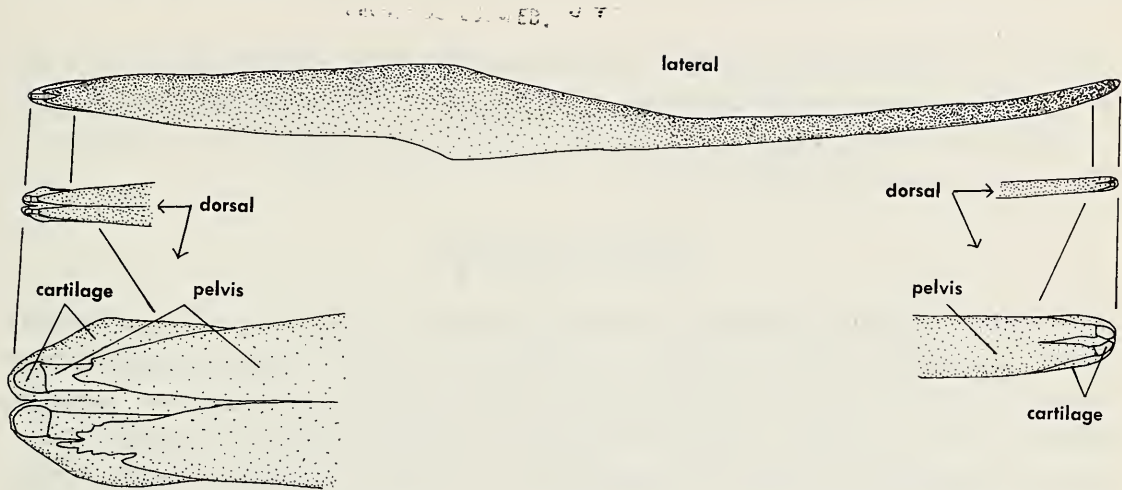
Fig. 5. Pelvis of *Triodon macropterus*, ANSP 98917, 463.3 mm SL. Above, lateral view of the entire pelvis (178 mm length); middle, dorsal views of the anterior and posterior ends of the pelvis; below, enlargements of the dorsal views of the anterior and posterior ends of the pelvis.

the extreme posterior end). The structure of the paired plugs is basically similar at both ends of the pelvis, although far larger at the anterior end. Therefore, Tyler does not believe that the paired plug at the posterior end of the pelvis in *Triodon* is necessarily homologous to the far more complex and less distinctly paired plug supporting the highly modified fin ray element in balistoids.

Examination of an additional specimen of the rarely collected *Triodon* (NSMT-P 3415, 370.0 mm SL) by Matsuura shows the same structure of the pelvis and cartilages as in Tyler's specimen. However, Matsuura believes that the plug at the posterior end of the pelvis of *Triodon* is possibly homologous to the cartilaginous plug of the fin ray element of balistoids for the following reasons: 1) the condition of the plug in *Triodon* is closely similar to that of such advanced monacanthids as *Pseudalutarius* and *Oxymonacanthus,* except for being paired; 2) the paired nature of the plug in *Triodon* is related to the divided condition of the pelvis, while the single plug of monacanthids corresponds to the undivided pelvis of that family; 3) the advanced monacanthids have a cartilaginous region at the anterior end of the pelvis similar to that of *Triodon.*

Only detailed histological analysis of the ontogenetic development of these cartilagenous plugs in *Triodon* and balistoids will solve the question of their possible homology.

Summary

The majority of the osteological observations that were made independently by Matsuura (1979) and Tyler (1980) on a largely similar coverage of

genera and species of balistoids are compatible. Most of the differences are due to statements made about genera based on different sets of species examined or about species based on different sized specimens examined, and on other intraspecific variation.

Acknowledgments

Literature Cited

Fraser-Brunner, A. 1935. Notes on the plectognath fishes.—I. A synopsis of the genera of the Family Balistidae.—Ann. Mag. Nat. Hist. (10)15:658–663.
Matsuura, Keiichi. 1979. Phylogeny of the Superfamily Balistoidea (Pisces: Tetraodontiformes).—Mem. Fac. Fish., Hokkaido Univ. 26(1/2):49–169.
Tyler, James C. 1962. The pelvis and pelvic fin of plectognath fishes; a study in reduction.—Proc. Acad. Nat. Sci. Philadelphia 114(7):207–250.
———. 1980. Osteology, phylogeny and higher classification of the fishes of the Order Plectognathi (Tetraodontiformes).—U.S. Dep. Commerce, Nat. Ocean. Atmos. Admin., Nat. Mar. Fish. Serv., NOAA Tech. Rep., NMFS Circ. 434, 422 pp.

(JCT) Division of Environmental Biology, National Science Foundation, Washington, D.C. 20550, U.S.A. (Research Associate, American Museum of Natural History, Department of Ichthyology, and U.S. National Museum of Natural History, Department of Vertebrate Zoology), and (KM) Department of Zoology, National Science Museum (Natural History Institute), 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 160, Japan.